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US ARMY MEDICAL RESEARCH LABORATORY

FORT KNOX, KENTUCKY

REPORT NO. 376
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DERIVATION OF 'SUBJECTIVE VELOCITY' FROM ANGULAR-DISPLACEMENT ESTIMATES MADE DURING PROLONGED ANGULAR ACCELERATIONS: ADAPTATION EFFECTS*

*Task under Psychophysiological Studies, USAMRL Project No. 6-95-20-001, Task, Studies of Vestibular Functions.

UNITED STATES ARMY
MEDICAL RESEARCH AND DEVELOPMENT COMMAND

REPORT NO. 376

DERIVATION OF 'SUBJECTIVE VELOCITY' FROM ANGULAR-DISPLACEMENT ESTIMATES MADE DURING PROLONGED ANGULAR ACCELERATIONS: ADAPTATION EFFECTS*

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*Task under Psychophysiological Studies, USAMRL Project No. 6-95-20-001, Task, Studies of Vestibular Functions.

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ABSTRACT

DERIVATION OF 'SUBJECTIVE VELOCITY' FROM ANGULAR-DISPLACEMENT ESTIMATES MADE DURING PROLONGED ANGULAR ACCELERATIONS: ADAPTATION EFFECTS

OBJECT

To ascertain the intensity of the subjective vestibular reaction throughout prolonged angular accelerations of various magnitudes.

SUMMARY AND CONCLUSIONS

Subjective velocity, as measured, first rises and then declines during the course of a constant angular acceleration. Within the range of stimuli applied, 'rise' time to maximum subjective velocity appears to be constant regardless of the magnitude of the stimulus. The maximum attained and the rate of change of subjective velocity up to its maximum during a prolonged constant angular acceleration are directly related to the magnitude of the angular acceleration. These characteristics of the subjective reaction are fairly well predicted by Van Egmond's 'torsion-pendulum theory', however a pronounced decline in subjective velocity which occurs after approximately 30 sec of a prolonged constant angular acceleration cannot be accounted for by the theory. This decline indicates the presence of an adaptation effect in the vestibular system.

RECOMMENDATIONS

Further experimentation to improve the method of estimating the intensity of the subjective vestibular reaction, utilization of the method to study the carry over of adaptation effects from one stimulus to the next, utilization of the method to study individuals with clinically diagnosed malfunction of the vestibular system and utilization of the method to study the effects of motion sickness preventive drugs on vestibular sensitivity are recommended.

Submitted 21 November 1958 by:

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I. INTRODUCTION

Although previous experiments have suggested the presence of adaptation in the vestibular system (1, 6, 9, 10, 13, 18), the only descriptions of the development and recovery of apparent adaptation effects in the subjective vestibular reaction are based upon studies of the changes in duration of the vestibular reaction under various stimulus conditions (9, 10). To obtain a better estimate of the magnitude of these effects than that which can be provided by studying the time characteristics of the reaction, it is desirable to have an estimate of the intensity of the reaction, throughout its course.

The subjective experience accompanying vestibular stimulation by angular acceleration has magnitude and direction. For example, a blindfolded person at the center of a turn-table, during a low-magnitude, constant, angular acceleration, feels, after a short latency, that he is rotating. As the acceleration continues (within certain time limits) he feels that he is rotating "faster." After the stimulus terminates, his rate of apparent rotation becomes progressively lower until it reaches zero magnitude. If the stimulus is stronger (higher magnitude angular acceleration), the experienced rate of rotation attained is greater per unit time, within limits. If the direction of the acceleration is reversed, the direction of the experienced rotation is reversed. Hence, the subjective experience has both magnitude and direction, and therefore the vector notation, velocity, is appropriate. Since the velocity refers to rotatory motion about a fixed axis, without the translation implied by linear velocity, the terms - subjective angular velocity - seem appropriate. However, as a matter of convenience, this will be shortened to - subjective velocity.

In certain sections of this report, magnitudes are averaged without regard to direction. Whenever this is done, the scalar notation, subjective speed, is used.

There are a number of possible methods of estimating subjective velocity (1, 7). One of these, suggested by Hood (3), is particularly interesting because it incorporates a technique analogous to that of the Bekesy Audiometer test for hearing. A visual target is given a velocity relative to the subject which fluctuates in magnitude about some base velocity. The direction and magnitude of the base velocity is adjusted by the subject so that "real and illusory" motions of the light are opposed (3), and so that the peak velocities of the fluctuating "real motion" just exceeds the opposing velocity of the "illusory motion." This presumably produces a series of brief "real movements" opposite in direction to the cancelled "illusory motion" (the latter being part of the vestibular reaction). As the "illusory motion" declines, the base velocity of the subject-controlled "real motion" would supposedly decline in a like manner. Although this method may be quite valuable for the estimation of subjective velocity, the method itself and the results it yields have not yet been described in sufficient detail for a comparative evaluation.

A method which is somewhat similar was tried in this laboratory. The subject, rotated in a dark room, was asked to move a visual target through an arc to exactly compensate for his experience of apparent bodily rotation, in other words, to keep the angular displacement of the light fixed with respect to the outside world (which he could not see). At the limit of the excursion, which was arbitrarily set at 90° the subject rapidly returned the light to center and then recommenced the slow compensatory tracking. Hence, a kind of manual nystagmus with counterparts of the slow and fast phases of vestibular ocular nystagmus was set up. This method gave results very similar to the results obtained by the method eventually chosen in the present study, but a few subjects showed pronounced habituation effects with this method. In view of evidence indicating that habituation is influenced by an interaction between the visual and vestibular systems (2, 8) this method, which forces a voluntary, visual pursuit during the normal period of vestibular nystagmus, was discarded, for the present study at least.

The method selected to estimate subjective velocity in the present experiment is based upon subjective estimates of angular displacement, a method previously used by Groen and Jongkees (7) and Bekesy (1). The subject's task is to signal each time he feels that he has rotated through a given angle. Time between any two adjacent signals should then be inversely proportional to the average subjective velocity within the interval if the subjective velocity or the rate of change of subjective velocity is approximately constant. With the assumption that a subject can maintain a fairly constant concept of an angular displacement such as 45°, 90°, 180°, or 360°, subjective angular velocity may be plotted with respect to time throughout the course of the reaction.

The principal objective of the present study is 1) to provide a description of the change in the intensity of the subjective reaction, i.e., the magnitude of the subjective velocity, during periods of prolonged, constant angular accelerations which are varied in magnitude from one period of stimulation to the next, and 2) to determine the nature of any response decline during the course of a constant-magnitude stimulus.

II. DESCRIPTION OF EXPERIMENT

The rotation apparatus and enclosure have been described in detail in previous reports (11). The subject was positioned with his head at the center of rotation facing a small tri-dimensional target light (5) located at a distance of 1 meter at eye level. The faint target light, which did not make the room walls visible, was used principally to facilitate the subject's job of reporting apparent rotation effects.

Subjects were instructed to concentrate on the apparent rotation of the light and to signal the direction of apparent rotation as soon as it commenced and to signal thereafter each time they had apparently rotated through 45°.

Each subject received a practice session which began by rotating the subject slowly (6 deg/sec) in full-room illumination to reveal black, vertical stripes marking off 45° arcs on the circular wall of the enclosure. The subject was told that the room lights would be off during the experiment and that he would be required to signal each time a 45° arc was apparently traversed, i.e., each time he imagined himself passing one of the 45° markers. Subjects were further instructed to concentrate particularly on the apparent rotation of the target light and to ignore, if possible, other cues to speed such as noise and slight, but present, vibratory cues. It is to be emphasized that these extraneous cues did not provide information regarding the direction of rotation but could be used as clues to angular speed. That the subjects were not entirely successful in ignoring these extra cues will be clearly demonstrated in the results section. However, the experiment was designed to provide an indication of the magnitude of the influence of these extraneous cues.

Following the instruction trial with full-room illumination, four practice trials were administered under regular experimental conditions, i.e., with the room in darkness except for the target light, to ascertain whether the subject considered himself capable of following instructions. During these practice trials it was also necessary to determine whether or not the 45° arc was convenient from the subject's point of view. Previous investigation (1, 7) and our own pilot studies had indicated that individual differences in subjective velocity might necessitate the use of a greater subjective displacement between signals; e.g., where subjective velocity is so high that the subject is required to signal 45° displacements too rapidly to make, what he considers, a reasonable estimate of 45°, it is desirable to change to a 90° or 180° displacement. None of the subjects of the present experiment indicated that they felt overtaxed by the 45° judgments within the range of angular accelerations used in this study.

An indication of the stimulus situation for the experimental trials is presented in Figure 1. Each experimental trial was commenced by a brief (2 sec) acceleration to an angular velocity of 6 deg/sec (base speed) which was maintained 30 sec beyond cessation of the primary subjective effect of this initial acceleration. The base speed was used to provide optimum control of the acceleration of the turntable. At the end of the 30-sec "rest interval," a prolonged constant angular acceleration of predetermined magnitude and duration was commenced. When this acceleration terminated or when the subject signaled cessation of the primary effects of the acceleration (whichever occurred last), a 60-sec period of constant velocity was commenced.

After the "rest period" at constant velocity, a constant angular deceleration of the same magnitude and duration as the previous acceleration was commenced so that the subject was returned to base velocity. When the primary effects of this deceleration ceased, the turntable was stopped and the trial was considered ended.

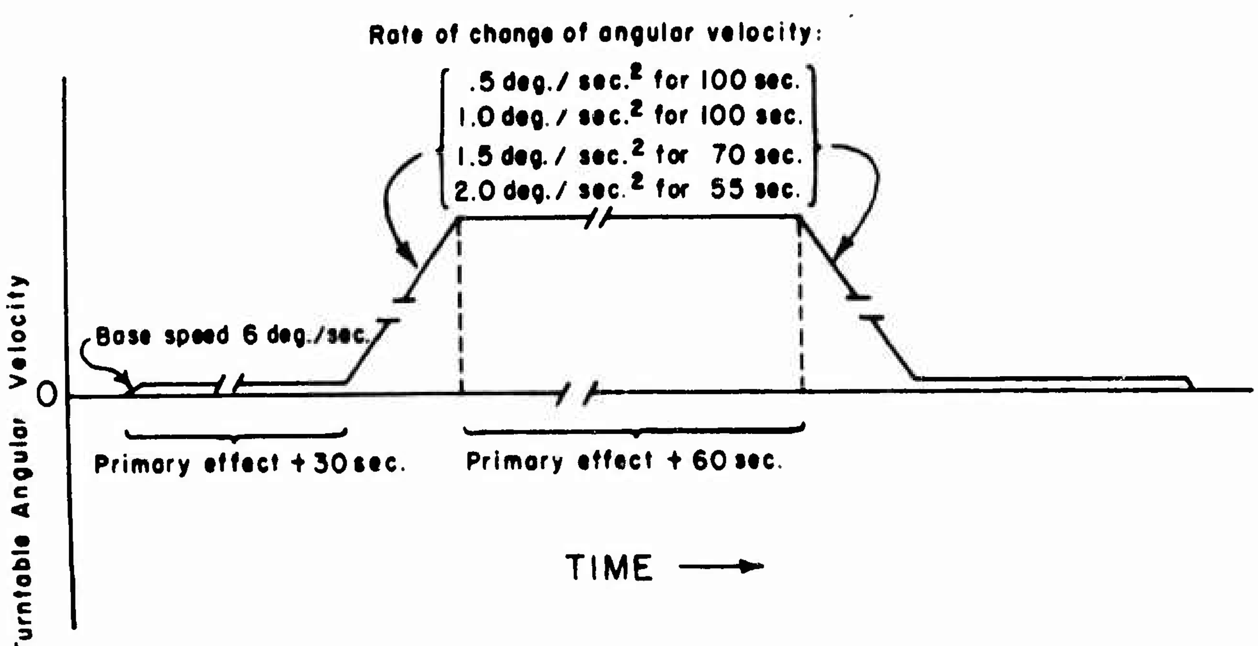

Fig. 1. Diagram showing the stimulus situation for a single experimental trial.

Four magnitudes of the prolonged angular acceleration and corresponding prolonged angular deceleration were used. They were 0.5, 1.0, 1.5, and 2.0 deg/sec^2 maintained respectively 100, 100, 70, and 55 sec. Each of the 10 subjects received one trial at each stimulus magnitude in each of four experimental sessions held on separate days. In addition, there was a single warmup trial at the beginning of each experimental session. The four practice trials described above were given one or two days before the first experimental session.

The various stimulus magnitudes were presented in counterbalanced orders so that any mean response differences between magnitudes of stimuli would not be attributable to order effects. Between the 1st and 2nd trials and between the 3rd and 4th trials, subjects were given a rest interval of at least one min at zero angular velocity with full-room illumination. Between the 2nd and 3rd trials a similar rest interval of at least 3 min duration was given during which the subject was encouraged to leave the turntable.

III. RESULTS

A. Main Effects

The overall results are represented in Figure 2 where successive points in each curve are respectively mean subjective speeds based on all experimental trials of all subjects within successive 5-sec intervals of the total period of application of a particular stimulus magnitude irrespective of whether the stimulus was an acceleration or a deceleration. Hence, each of the four curves represents the mean results for one of the magnitudes of the stimuli employed in the experiment.

Figure 2 shows clearly that there are increases in the rate of change of subjective speed and also in the maximum subjective speed attained with each increase in angular acceleration. It is also apparent in Figure 2 that subjective speed reaches a maximum in approximately 30 sec, after which subjective speed declines even though the angular acceleration is maintained constant. In other words, the magnitude of the maximum subjective speed attained is dependent upon the magnitude of the stimulus; the length of time required to reach the maximum subjective speed during a constant-magnitude stimulus appears constant regardless of the stimulus magnitude; a decline in response magnitude during constant-magnitude stimulus is present with all magnitudes of the stimulus employed in the

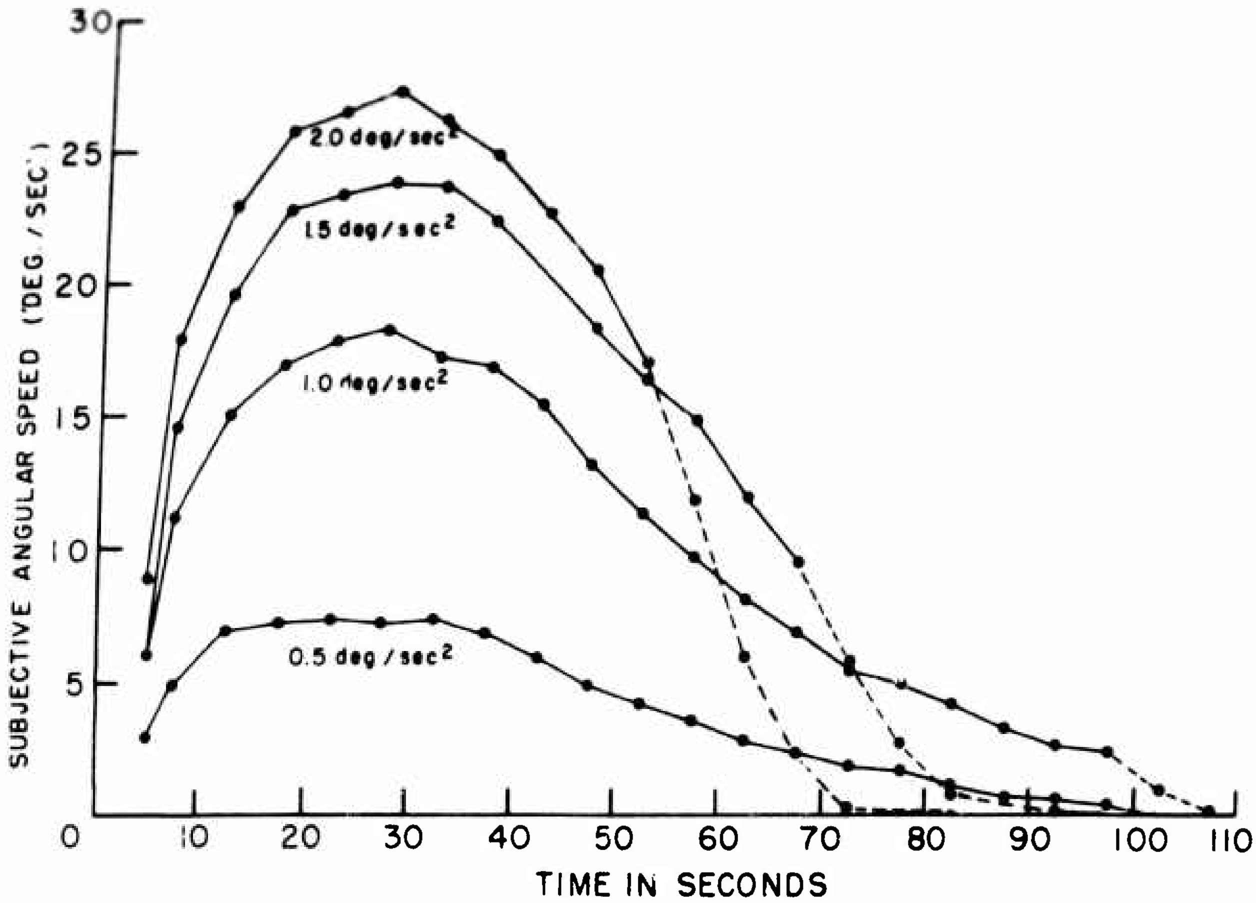

Fig. 2. Subjective angular speed with respect time during each of four stimuli of different magnitudes. Dotted lines show reaction after constant magnitude stimulus terminates. Data for same magnitude accelerations and decelerations were averaged in this figure.

experiment, and time of onset of the decline appears to be constant regardless of the stimulus magnitude.

B. <u>Effects of Extraneous Stimuli</u>

Figure 3 presents subjective velocity plotted with respect to time for the various angular accelerations used in the experiment, and Figure 4 presents the same information for the various angular decelerations. (Figure 2 is actually an average of Figures 3 and 4, i. e., subjective velocities of corresponding time intervals and stimulus magnitudes in Figures 3 and 4 were averaged to obtain the curves presented in Figure 2.) Note especially that the times taken to reach the maxima and the magnitudes of the maxima attained are greater

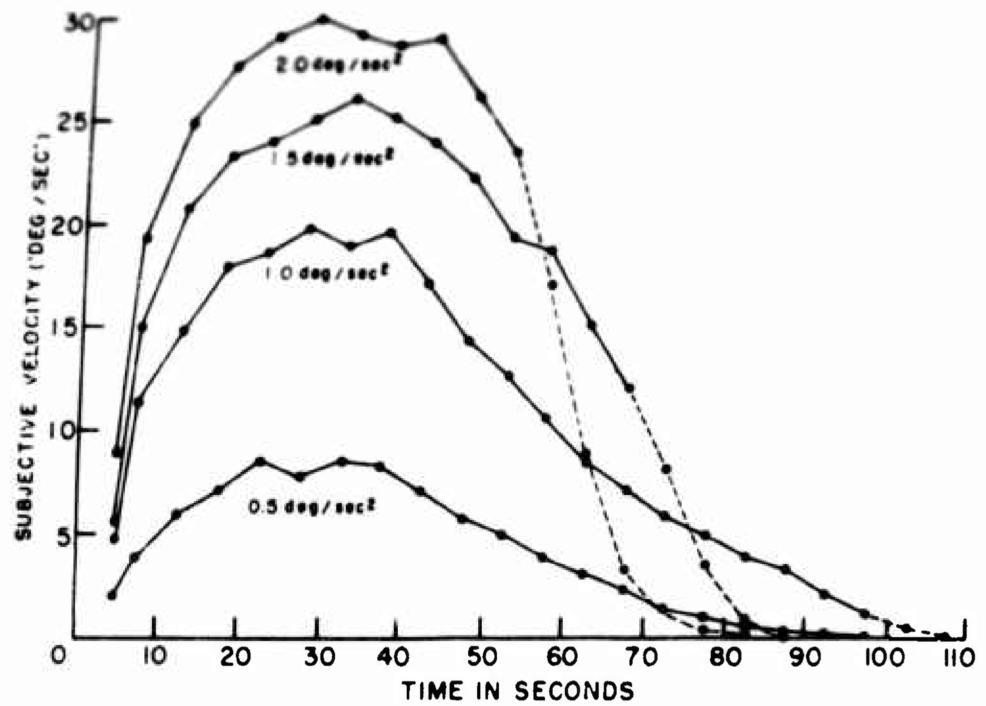

Fig. 3. Subjective angular velocity with respect to time during each of four constant magnitude angular accelerations. Dotted lines show reactions after acceleration terminates.

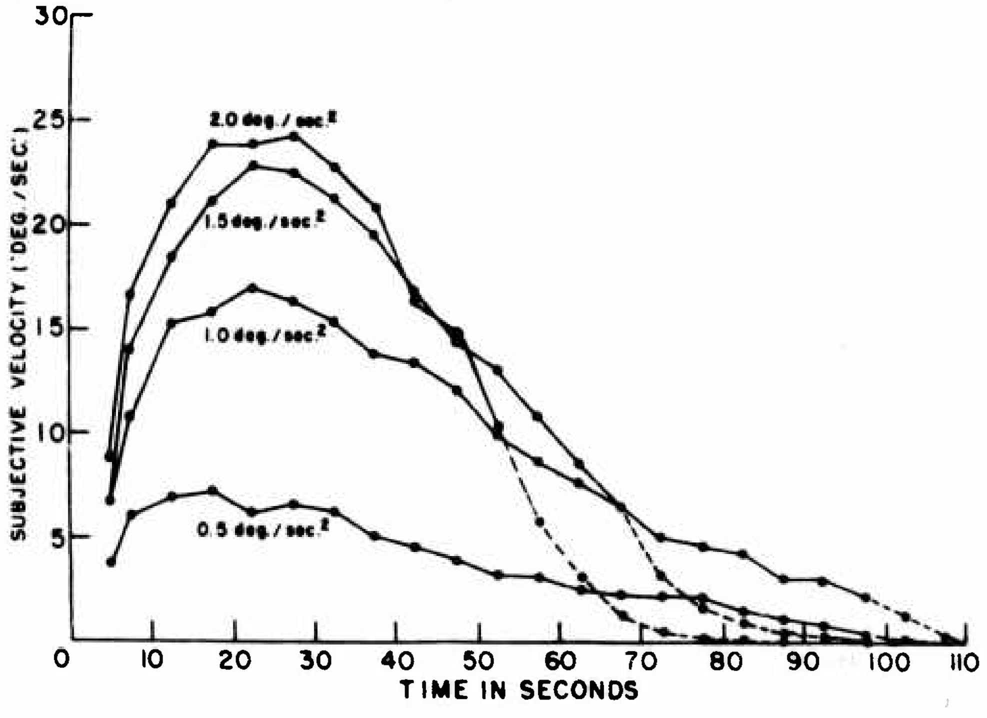

Fig. 4. Subjective velocity with respect to time during each of four constant magnitude angular decelerations. Dotted lines show reaction after deceleration terminates.

for acceleratations than for the corresponding decelerations. (Compare Figures 3 and 4 and see Table 1.)

These differences in results between comparable magnitudes of acceleration and deceleration reflect the influence of the extraneous cues mentioned earlier. That is, during angular acceleration the subject can detect an increase in speed by auditory and vibratory cues. These combine with the vestibular information to produce a higher subjective velocity than would be attained from the vestibular information alone. Note, however, that although these extraneous cues continue to indicate increasing speed throughout the period of acceleration, the subjective velocity in each case reaches a maximum and then declines during the acceleration. The decline in subjective velocity while the extraneous cues are still increasing suggests that the vestibular information which is declining (due to some adaptation-like process) is the primary basis for the subject's estimates of subjective velocity.

TABLE 1

RESPONSE MAXIMA, TIME REQUIRED TO ATTAIN ESTIMATED RESPONSE MAXIMA AND STANDARD DEVIATION OF RESPONSE MEASURES AT MAXIMA FOR EACH MAGNITUDE ANGULAR ACCELERATION AND DECELERATION

Stimulus Magnitude*	0.5		1.0		1.5		2.0	
Stimulus Direction	Accel	Decel	Accel	Decel	Accel	Decel	Accel	Decel
Response Max**	9	7	20	17	26	23	30	25
SD Of Response at Max**	5.0	4.8	8.8	8.3	12.8	9.3	10.7	10.0
Time to Max Response***	25.0	18.0	27.5	22.5	32.0	22.5	27.5	22.5

*deg/sec^2 **deg/sec ***sec

During deceleration, the subject experiences apparent rotation opposite in direction to the actual rotation of the turntable. For a period of approximately 20 sec, the subjective velocity continues to increase even though the turntable velocity is actually decreasing. This means that the extraneous auditory and vibratory cues, which now indicate decreasing speed while the subjective velocity is increasing, are sufficient to overcome the vestibular information under the conditions of the experiment. However, the differences between acceleration and deceleration in maximum subjective velocities attained and the difference in times taken to reach these maxima are almost certainly indicative of the influence of these extraneous cues.

C. Change in Rate of Decline When Stimulus Terminates

A point of interest in Figures 2, 3, and 4 is the increased rate of decline of the subjective velocity after the stimulus terminates (the dotted lines). It will be recalled that the 1.5 deg/sec^2 stimulus and 2.0 deg/sec^2 stimulus were maintained for 70 sec, and 55 sec, respectively. The plotted points after termination of these two stimuli show an increased rate of decline in response and this corresponds temporally to a point in time when the cupula has theoretically commenced its return to its "non-stimulating" position. It can be seen that the response has already begun a decline, apparently due to adaptation, during the stimulus and when the stimulus terminates, the response begins dropping more sharply presumably due to decreased neural input resulting from decreased cupula displacement. Each of the 0.5 and 1.0 deg/sec^2 stimuli were maintained for 100 sec. The magnitude of response is too low at 100 sec in the case of the 0.5 deg/sec^2 stimulus to show a similar effect, but the response to the 1.0 deg/sec^2 stimulus, although very low at 100 sec, is sufficient to show the increased rate of decline after the stimulus terminates. Presumably if the 1.5 and 2.0 deg/sec^2 stimuli had been maintained for 100 sec, the decay curves for these stimuli from 55 sec to 100 sec would have been more similar to those obtained with the 0.5 and 1.0 deg/sec^2 stimuli, i.e., would not have exhibited the sharp decline after 70 sec, and 55 sec, respectively.

D. Individual Differences

Table 2 presents a comparison of two subjects who represent the upper and lower extremes of the group of 10 subjects in regard to magnitudes of subjective velocities with the various stimuli. Note that the responses of subject HH for the 2.0 deg/sec^2 stimulus are approximately the same as the responses of subject PC for the 0.5 deg/sec^2 stimulus. This, as well as the standard deviations in Table 1, indicate that there are considerable overlaps in the distributions for each of the corresponding points in the curves presented in Figure 2.

However, subject HH and subject PC considered independently of one another show clearcut differences in magnitudes of subjective velocity and rate of change of subjective velocity from one stimulus magnitude to the next. This is apparent in Table 2. Moreover, curves plotted for all subjects and for each magnitude of the stimulus showed 1) that subjective velocity in every case first increased, then reached a maximum then decreased during each stimulus, and 2) that rate of change of subjective velocity and maximum subjective velocity attained, also in every case, were greater when magnitude of the stimulus was greater; i.e., these aspects of the response were directly related to magnitude of the stimuli. The similarity of the form of the curves from one subject to the next and the clear separations of the curves obtained from the different stimulus magnitudes with each subject indicated that the average curves presented in Figure 2 differ reliably from one another even though the standard deviations in Table 1 and the overlapping distributions indicated in Table 2 would seem to call this into question. Whether these individual differences are attributable to differences between subjects in conceptualizing 45° or to differences in subjective velocity is open to question.

TABLE 2

SUBJECTS HH AND PC WHO YIELDED RESPECTIVELY THE LOWER AND UPPER LIMITS OF SUBJECTIVE VELOCITIES OBTAINED DURING EACH OF THE STIMULI OF DIFFERENT MAGNITUDES.

Subject	HH				PC			
Stim Mag deg/sec^2	.5	1.0	1.5	2.0	.5	1.0	1.5	2.0
Av. Subjective Velocity (deg/sec) during interval:								
0 - 5	1.5	1.3	4.7	4.5	2.5	2.8	7.6	11.3
5 - 10	2.8	5.0	7.3	10.1	9.7	13.9	20.5	24.2
10 - 15	3.0	5.3	8.5	13.0	13.4	18.5	28.2	34.6
15 - 20	2.6	5.8	12.3	15.5	14.7	22.8	30.7	37.8
20 - 25	3.0	6.7	11.2	16.5	14.1	26.7	31.3	42.5
25 - 30	3.6	6.8	13.8	15.6	14.4	28.8	34.0	42.5
30 - 35	3.9	6.8	11.8	13.6	14.3	30.0	38.0	45.3
35 - 40	3.7	6.9	11.6	13.5	15.0	29.2	33.8	40.9
40 - 45	3.5	6.5	9.0	11.7	13.0	24.8	30.2	39.4
45 - 50	2.7	6.4	9.5	10.5	9.8	21.0	24.7	34.3
50 - 55	2.9	5.4	7.8	9.4	8.6	15.8	24.7	30.9

E. Habituation Effects

Repetitive exposure to discrete periods of prolonged rotation can produce attenuated vestibular reactions. Although this was not a primary point of investigation in the present experiment, the effects of repetitive stimulation can be ascertained by comparing the first and the fourth sessions of the experiment. Clear differences in results between these two sessions, typified by the data for the 1 deg/sec^2 stimulus presented in Figure 5, were obtained with each magnitude of stimulus employed. Without question, there were carry-over effects from day to day which resulted in the reduction of the magnitude of subjective velocity as the experiment progressed.

Fortunately, these effects did not obscure the effects of primary interest in the experiment. As Figure 5 shows, the rise and fall of subjective velocity were equally apparent during a constant-magnitude stimulus in the first and fourth sessions, although the subjective velocities are uniformly attenuated in the fourth session.

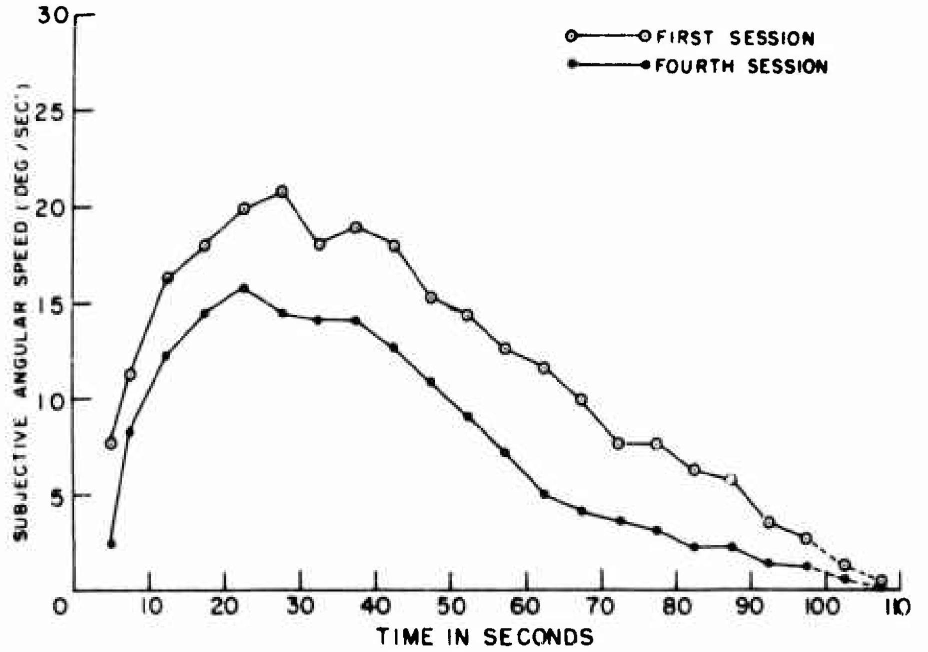

Fig. 5. Subjective angular speed with respect to time during the 1.0 deg/sec^2 stimulus. Results of first and fourth sessions compared.

IV. DISCUSSION

The variations of subjective velocity with respect to time, during constant angular acceleration, have a number of properties of theoretical significance. Some of these properties, and their possible dependence upon psychophysical method, are discussed below.

The assumption has been made frequently (4, 7, 13, 15) that intensity of the vestibular reaction is directly proportional to angular displacement of the cupula and that cupula angular displacement, x, is approximately described by:

$$x = a\,(1 - e^{-rt}) \tag{1}$$

where a is the magnitude of the stimulus (constant angular acceleration), t is the stimulus duration, and r is a constant estimated to be approximately 0.1 by Van Egmond et al (4).

A. Time Constant of Equation (1)

With a value of $r = 0.1$, the time constant of equation (1), $1/r$, is approximately 10 sec. This means, among other things, that 93.6% of maximum cupula displacement for a given magnitude a should be reached in 27.5 sec and that the 63.2% of maximum should be reached in 10 sec and further that these respective times to 0.936 max and to 0.632 max should be independent of the magnitude of the acceleration. If response intensity (subjective velocity in this case) is directly proportional to magnitude of the angular displacement of the cupula, these same predictions should hold for subjective velocity.

Figure 2 shows that the time elapsed to the point of maximum subjective velocity is in fact roughly constant from one magnitude of acceleration to the next, and that these maxima are attained between 25 and 30 sec, i.e., at about 27.5 sec.

The time constant, $1/r$, can be estimated for each a from their respective curves in Figure 2 by finding the values of t which correspond to subjective velocities equal to 63.2% of their respective maxima. Assuming that the subjective velocity attained at 27.5 sec is 93.6% of the maximum which would have been attained without adaptation effects, adjusted maxima can be estimated by dividing the observed maxima by .936. Table 3 presents values of $1/r$ estimated from the observed maxima and from the adjusted maxima.

The values of $1/r$ are less than the value of 10 estimated by Van Egmond (4). This means that at 10 sec of acceleration, the subjective velocity for each magnitude of acceleration employed is greater than 63.2% of even the adjusted maximum. In view of the abundant evidence (1, 6, 9, 10, 13, 17, 18), that the vestibular response is diminished by adaptation effects and that these effects become more pronounced with more prolonged stimuli (9, 10), the magnitude of the

TABLE 3

ESTIMATES OF THE CONSTANT 1/r FROM EACH MAGNITUDE STIMULUS USED

Stimulus (deg/sec^2)	.5	1.0	1.5	2.0
From Observed Maximum	7.5	8.0	8.0	6.5
From Adjusted Maximum	8.2	9.0	8.9	7.9

observed vestibular reaction is probably much more attenuated by adaptation at 27.5 sec than at 10 sec.

Hence, the present procedure, which was specifically designed to yield adaptation effects by use of prolonged, constant stimuli, should not be expected to provide estimates of 1/r uncontaminated by adaptation. It is even likely that Van Egmond's procedure for estimating this constant from subjective reactions involved some reaction attenuation due to adaptation. For example, any acceleration, sufficient to produce a marked cupula deflection, which is not followed by deceleration to effect a recovery, is sufficient to maintain the activity of the vestibular system an abnormally long time by virtue of the slow return of the cupula to its resting position by its own elasticity. Therefore, the duration of the more prolonged reactions in cupulograms are probably shortened by adaptation effects (9, 10) which would reduce the slope of the cupulogram (3, 7, 20). This would have lowered Van Egmond's estimates of 1/r, a possibility which is recognized by these authors (personal communication with Groen).

Lowenstein (16, 17) has found in elasmobranch that increasing the intensity of stimulation (galvanic or rotational stimulus) of the ampullar mechanism "brings in one after the other previously silent units of higher threshold." These units often adapt themselves rather rapidly, and fire over a limited range of stimulus intensity only. At rest, i.e., without stimulation, other elements fire spontaneously and these are "delicately poised to react to the slightest cupula movement by a change in the rate of an already existing discharge activity." Lowenstein assumes that these sensitive elements, since they are spontaneously active, are either nonadapting or very slowly adapting. A gradient of susceptibility to adaptation with elements which are successively recruited as the cupula is deflected has interesting implications. For example, assume that we have a number of groups of elements, A, B, and C which are recruited in the order listed with increasing cupula deflection. With a constant angular acceleration which only gradually activates Group C (as when the cupula is approaching its asymptote for a given α), by the time Group C is activated, Group B may be adapted, and the proportionality between total neural activity and cupula deflection would be altered. On the other hand, a briefer but stronger stimulus which activates all three groups of elements rapidly should produce 1) a stronger reaction with the same cupula deflection and 2) total neural activity which more nearly maintains a constant proportionality to cupula deflection.

Such an explanation could account for the low values of $1/r$ estimated from the present results and would further predict that higher-magnitude stimuli maintained for 30 sec or longer should yield a lowered ratio of maximum subjective velocity to magnitude of acceleration. The present results are suggestive of the lowering of this ratio with the 2 deg/sec^2 stimulus (Fig. 6) but a considerable extension of the range of accelerations used would be necessary to test this notion, particularly in view

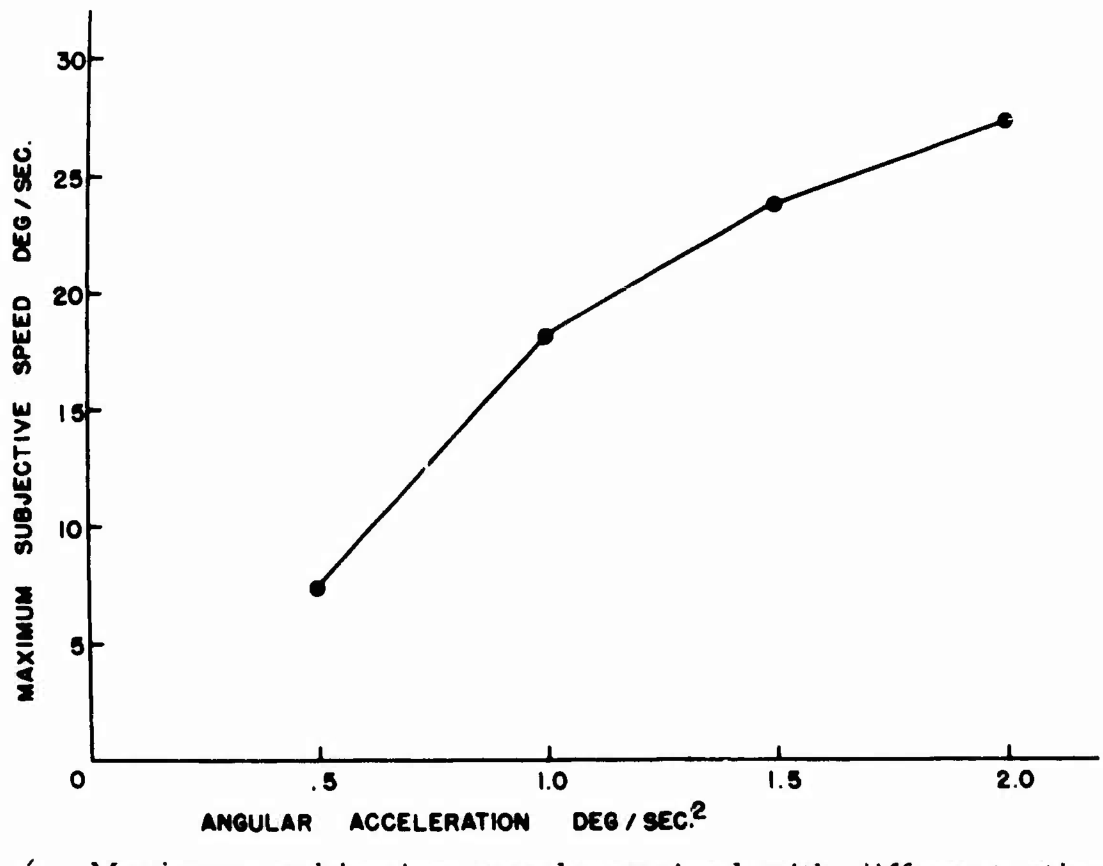

Fig. 6. Maximum subjective speeds attained with different stimulus magnitudes. Data were averaged over acceleration and deceleration for each stimulus magnitude.

of three considerations: 1) the present data do not furnish enough points to establish the downward trend of this ratio; 2) a 2 deg/sec^2 stimulus applied indefinitely probably produces a maximum cupula deflection which is only a small percentage of the possible cupula deflection with stronger stimuli; 3) it is possible that the method employed restricted the maximum subjective velocities obtained. An experiment in progress involving higher angular accelerations, and including an investigation of the influence of the size of the angle estimated on subjective velocity should help clarify these issues.

B. Decline in Subjective Velocity During Constant Angular Acceleration

Although the assumed relationship between equation (1), cupula position, and subjective velocity is called into question by the previous section, the decline in subjective velocity during constant angular acceleration apparent where $t > 27.5$ sec demonstrates clearly that at least beyond this time limit, equation (1) is an indequate basis for prediction of subjective velocity. According to equation (1), subjective velocity should approach its maximum asymotically and should not decline during a constant angular acceleration. That this rise-and-fall phenomenon is not merely an artifact of the technique of angle estimation used herein is indicated by the following:

1. A number of subjects in this and previous experiments occasionally indicated that the primary subjective reaction terminated during the stimulus. These and other subjects were questioned and all of their descriptions leave little doubt as to the rise and fall of subjective velocity during constant angular acceleration.

2. A series of experiments (9, 10), utilizing response duration as a dependent variable led to the conclusion that the magnitude of the primary subjective reaction must decline during a very prolonged, constant stimulus.

3. In preliminary experiments, another estimation technique was tried, namely requiring the subject to continuously estimate his angular velocity as being greater than, equal to, or less than the immediately preceding angular velocity. The subject manipulated a small circular dial such that its angular displacement from an arbitrary zero position was, for the respective judgments just mentioned, increased, held constant, or decreased. This method gave curves during and after constant, angular accelerations which were surprisingly similar in form to those shown in Figure 2. This method has the advantage of eliminating assumptions about the subject's ability to estimate angular displacements or to maintain a constant concept of subjective angular displacement. Unfortunately, the method does not provide estimation of the magnitude of subjective velocity at any point

in the reaction. Since the two methods seemed to yield similar response curves, the angular-displacement estimation technique was chosen. However, the "rise and fall" of subjective velocity during a constant stimulus is clearly demonstrated by this alternative method.

The fact that subjective velocity declines during a constant, angular acceleration clearly indicates the intrusion of a process which complicates the theoretical relationship between cupula displacement and subjective velocity. A mechanism such as that suggested above probably could and certainly should also explain this aspect of the results, i. e., later recruited elements drop out quickly due to rapid adaptation, early recruited elements also eventually drop out because they are maintained in heightened activity longer.

If the apparent adaptation effects encountered in the present results are attributable to reduced neural output from the end-organ, as the explanation based upon Lowenstein's work (16, 17) would suggest, then it would seem that the ocular nystagmic reaction should demonstrate similar changes during prolonged reactions. There is evidence indicating that these two aspects of the vestibular reaction may vary independently where the reaction is prolonged. Hulk, Groen, and Jongkees (15) have indicated that as stimulus strength increases to produce more prolonged after-reactions, the nystagmic after-reaction outlasts the subjective after-reaction. Some of the results obtained by Hauty (14) suggest, although his data are not completely consistent on this point, that the velocity of ocular nystagmus (slow phase) during constant angular accelerations increases for periods greater than the periods of increasing subjective velocity found herein, with the same magnitude stimuli.[1] If the nystagmic reaction does outlast the subjective reaction during

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[1]In contrast with Van Egmond et al (4) Hauty (14) did not find a systematic change in duration of the primary nystagmic after-reaction with graded stimuli. Graybiel and Hupp (5) found a systematic change in duration with graded stimuli, but the nystagmic reaction was not longer than the subjective reaction with stronger stimuli. Guedry, Peacock, and Cramer (12) found a longer nystagmic than subjective after-reaction with a stimulus which would produce a prolonged reaction. The common thread which seems to account for these apparent conflicts is visual-vestibular interaction. In Hauty's study and in the Guedry, Peacock, and Cramer study, nystagmus was recorded in complete darkness. In Van Egmond's studies, nystagmus was observed through Frenzl lenses so that possibilities for visual fixation were reduced or eliminated. In the Graybiel study, subjects observed a target light and reported the termination of its apparent motion while nystagmus was recorded. It may be that a reliable systematic relation between prolonged nystagmus after-reactions and stimulus magnitude is dependent upon visual feedback.

stimuli which produce prolonged reactions, then two questions arise: 1) Does vestibularly initiated nystagmus have its own perpetuating mechanism, in the absence of retarding visual and vestibular signals, which tends to maintain its velocity beyond the point where peripheral, neural input has already commenced to decline; or 2) is the subjective reaction selectively attenuated by an additional, central, attenuating mechanism which does not influence the nystagmic reaction? This point requires further experimental work for its eventual clarification.

Although the nature and locus of the process involved is debatable, one thing is apparent, viz., that the variation in subjective velocity with respect to time is not simply a linear function of cupula displacement with respect to time. This relationship is complicated by an adaptation-like process. The necessary and sufficient stimulus conditions for adaptation have not been established, but it is not unlikely that the magnitude and duration of cupula displacement and the cupula velocity are all relevant variables.

C. Other Characteristics of the Response

A number of characteristics of subjective velocity, as measured have been discussed. Some of the possible artifacts inherent in the method have been mentioned and it has not been established (and perhaps can never be established) that subjective velocity, as measured, represents with any known degree of quantitative percision, the actual experience of the subject.

However, a number of considerations suggest, at least, that the method used yields subjective velocities which may reflect subjective experience with some fidelity:

1. The response varies during a prolonged stimulus about as would be expected from other methods of obtaining knowledge of subjective velocity. This has been mentioned above.

2. Clear differences in the rate of change of subjective velocity were obtained with different magnitude accelerations. This is encouraging to say the least. Moreover, for the first 30 sec of the stimulus, the response varies about as would be expected from theory of the cupula mechanism. Deviations from precise expectations are possibly manifestations of an adaptation-like effect known to exist from previous experiments. The decline in subjective velocity after 30 sec of constant acceleration is, with little doubt, a manifestation of some such adaptation process.

3. At a point in time where the response was already decaying apparently due to adaptation, acceleration terminated and the subjective velocity immediately showed an increased rate of decay. (Subjects were not consciously aware, from extraneous cues, that acceleration had terminated.) Apparently the method is fairly sensitive to changes in subjective velocity.

4. For about the first 15 sec of the stimulus, the rate of change of subjective velocity corresponds fairly well with the rate of change of velocity of the turntable. During this period, the magnitude of subjective velocity would correspond fairly well with the magnitude of turntable velocity, if the turntable acceleration had been initiated from zero velocity (rather than, for example, from 6 deg/sec in the case of acceleration and 120 deg/sec in the case of some of the decelerations). Actually the subjective velocity as measured is slightly greater than the turntable velocity within the first 15 sec. This discrepancy, if it represents a true difference between subjective and turntable velocity would have some functional value for accurate position responses, i.e., the lag in the system, response latency, would be compensated by the heightened subjective velocity thereby giving a truer estimate of angular displacement.

V. SUMMARY AND CONCLUSIONS

Indications from previous experiments that the vestibular subjective reaction is diminished by an adaptation-like process during the course of a prolonged angular acceleration emphasizes the importance of having an estimate of the reaction throughout its course. Methods for estimating subjective velocity were discussed and the method selected is based upon subjective estimates of angular displacement.

Subjective velocity, as measured, first rises and then declines during the course of a constant angular acceleration. It is unlikely that the decline is an artifact of the method of measurement.

Rise time to maximum subjective velocity attained for a given stimulus appears to be constant regardless of the magnitude of the stimulus. Magnitude of the maximum subjective velocity attained and rate of change of subjective velocity up to the maximum subjective velocity during a prolonged angular acceleration are directly related to the magnitude of the angular acceleration. These characteristics of the response are fairly well predicted by Van Egmond's "torsion-pendulum theory" and can be used to estimate values for the time constant of the predictive equation. Such estimates agree fairly well with Van Egmond's original estimates and slight differences may be attributable to adaptation effects which were probably more effective in the present procedures than in those used by Van Egmond.

Maximum subjective velocity attained should be directly proportional to the magnitude of the stimulus and it appears that the ratio, maximum subjective velocity to acceleration-magnitude, declines with the higher magnitude accelerations. That this may be attributable to an artifact in the method of estimating subjective velocity is mentioned. An equally likely possibility is that adaptation effects differentially affect the maximum subjective velocities attained with different magnitude stimuli. This is based on the speculation that successively recruited groups of elements, with increasing cupula deflection, are progressively more susceptible to adaptation. Existing neurophysiological data support this notion.

That adaptation effects can be a partial determiner of response magnitude is clearly demonstrated by the decline in subjective velocity which commences during a constant magnitude stimulus after approximately 30 sec of stimulation. The possibility that a similar decline in the velocity of vestibular nystagmus will not occur after only 30 sec of constant angular acceleration with comparable magnitude stimuli is suggested by the work of other investigators. Some of the theoretical implications of this possibility are considered.

The data obtained indicate that the method of subjective angle estimation is a feasible method for estimating the magnitude of the subjective vestibular reaction.

VI. RECOMMENDATIONS

The following recommendations are made: 1) Further studies designed to ascertain attenuation of subjective velocity attributable to the method of subjective angle estimation. 2) Use of the method to ascertain the upper limits of the subjective velocity. 3) Use of the method to determine relative sensitivity of the vestibular apparatus when the head is in various positions of tilt with respect to the axis of rotation. 4) Use of the method to study the influence of drugs on the intensity of the vestibular reaction. 5) Use of the method with patients with vestibular disorders.

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